ENVIRONMENTAL FACTORS INFLUENCING ROOTING DAMAGE BY WILD PIGS AND EFFICACY OF POPULATION CONTROL FOR MITIGATING IMPACTS

By

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(Under the Direction of James C. Beasley)

ABSTRACT

As the distribution of wild pigs (*Sus scrofa*) continues to spread across its introduced range, landowners and managers are faced with the increasingly problematic task of maximizing the efficiency and efficacy of their control efforts. Despite the expanding distribution and extent of wild pig damage, there is little data regarding the impacts of control methods and the variability of damage in relation to season and habitat attributes. In this thesis, I monitored invasive wild pig populations, environmental rooting damage, and crop damage across 17 privately owned agricultural (POA) properties before and during control efforts in South Carolina, USA (Chapter 2). Additionally, I modeled the effect of season and habitat attributes on environmental rooting damage to unveil trends in rooting location and timing on both the POA properties and on the Savannah River Site (SRS), South Carolina, USA (Chapter 3). The results of this work will help landowners and managers decide when and where to utilize control efforts to maximize their effectiveness in an ever-changing landscape.

INDEX WORDS: Agricultural damage, habitat selection, Savannah River Site, *Sus scrofa*, wild pigs

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DEDICATION

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Wild pigs (*Sus scrofa*) were first introduced to North America by Spanish explorers in the 1500s, and while some small range expansions occurred, populations remained relatively localized for hundreds of years (Porter 2007; Mayer and Beasley 2018). In the early 1900's Eurasian wild boar were introduced in the southern United States for sport hunting (Barrett and Birmingham 1994) and eventually hybridized with escaped or released domestic pigs (Goedbloed et al. 2013). Today, wild pigs are estimated to be one of the most abundant and widespread invasive vertebrates in the United States, with a population estimated at 6.4 million and established populations in at least 38 states (Seward et al. 2004; Bevins et al. 2014; Mayer 2014; Snow et al. 2017; Mayer and Beasley 2018). Wild pigs are solely present throughout North America today due to human introductions; both intentional releases for sport hunting and subsistence, and by accidental means such as escapes from hunting ranches (Mayer and Brisbin 2009; Bevins et al. 2014). Wild pigs are extremely difficult to manage and exhibit nearly unchecked growth in their range expansion and population size (Keiter and Beasley 2017). This growth has placed a burden on local, state, and federal management efforts (Mayer and Brisbin 2009).

The success of wild pigs throughout their introduced range in the U.S. is due in part to having the largest reproductive potential of any large, free-ranging mammal in the U.S. (Taylor et al. 1998) and globally wild pigs are the most prolific breeder of any medium-sized mammal

(Mayer and Brisbin 2009). Pigs also are ecological generalists, which allows them to adapt quickly to new habitats and outcompete native species. Many populations in the southern regions of the U.S. reproduce year-round due to their remarkable ability to thrive in a diverse set of environmental conditions (Mayer and Brisbin 2009; Barrios-Garcia and Ballari 2012; Bevins et al. 2014). With the appropriate resources, on average a sow (female) can bear two litters per year but is physiologically able of having three litters in 14-16 months (Dzeicliolowski et al.1992; Waithman et al. 1999). A litter can have as many as 12 piglets, though a typical litter size is 4-6 (Taylor et al. 1998). Such a high reproduction rate is especially problematic in the U.S., as there are few or no predators of adult wild pigs throughout much of their range and juvenile survival is relatively high, especially after a few weeks of age (Keiter et al. 2017; Chinn et al. 2021). Predators such as coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) are known to feed on young, weak, or dead individuals, but are incapable of killing adult wild pigs (Tolleson et al.1995). Harvesting by humans is often the leading cause of mortality among monitored wild pig populations (Gabor et al. 1999; Hanson et al. 2009; Hayes et al. 2009; Servanty et al. 2011). Long-term research estimated higher annual survival rates in females than males, and in piglets when compared to adults (Toigo et al. 2008); this is attributed to intensive harvest of adult males for sport. Thus, recent studies have emphasized the importance of further research into juvenile recruitment in wild pigs (Bieber and Ruf 2005; Servanty et al. 2011; Mellish et al. 2014).

Studies on the diets of wild pigs have found that plant material makes up a large portion of the material consumed and is supplemented by invertebrate and vertebrate animals obtained through scavenging and predation (Massei and Genov 1996). Moreover, wild pigs are adapted to take reproductive advantage of pulses in food availability, such as hard mast (Loggins et al. 2002), through increased reproduction (Bieber and Ruf 2005). The success of wild pigs throughout the U.S. is also attributed to their highly varied omnivorous diet (Barrios-Garcia and Ballari 2012). Wild pigs compete with native wildlife and have been known to prey on birds, frogs, and small mammals (Wilcox and Van Vuren 2009), and are important scavengers of vertebrate carrion (Turner et al. 2017). Wild pigs also cause extensive damage to native ecosystems and agriculture through rooting behavior, where they overturn soil while foraging. This disruption of soil by rooting can lead to soil erosion, where it alters soil properties and damages the soil microbiome and soil layering (Barrios-Garcia and Ballari 2012). In addition to the effects of wild pigs on wildlife, they are documented to negatively affect water quality, which can impact native aquatic species (Kaller et al. 2007). Wild pigs also act as reservoirs for diseases that can infect livestock, humans, and wildlife, particularly with transboundary animal diseases such as African Swine Fever and Classical Swine Fever (Meng et al. 2009; Cleveland et al. 2017; Eckert et al. 2019; Luskin et al. 2020).

Movement behavior studies of wild pigs have shown the distribution of resources across a landscape is the main driver of wild pig movement (Gray et al. 2020). These studies have indicated seasonal availability of forage, vegetation cover, and other landscape features such as proximity to water determine habitat use, with wild pigs largely selecting for bottomland hardwood or similar wetland and riparian habitats, as well as areas with extensive canopy cover (McClure et al. 2015; Clontz et al. 2021). Wild pig rooting studies have generally found similar trends between habitat selection and changes in wild pig foraging locations, both being driven by the abundance and availability of more preferred foods such as fruits, seeds, grains, and certain plant material, while roots and bulbs are taken secondarily when other foods are unavailable (Welander 2000).

Wild pigs cause substantial damage and are considered ecosystem engineers for the role they play in shaping habitat (Boughton and Boughton 2014). In the U.S. alone, wild pigs are estimated to cause roughly $1.5 billion in damages each year. This figure includes roughly $800 million in agricultural damage to crops and livestock (Pimental et al. 2005; West et al. 2009). However, given the explosive growth in wild pig populations since 2005, the current economic impacts from wild pigs are likely substantially higher. For example, the expansion of the range and population size of wild pigs are also increasing the frequency of pig-vehicle collisions (Beasley et al. 2014). A landowner survey conducted in 11 southern U.S. states estimated annual damage to corn (*Zea mays*) and peanuts (*Arachis hypogaea*) at over $61 million and $40 million, respectively; these estimates do not include losses to peanuts in two states, South Carolina and Georgia (Anderson et al. 2016). Due to their generality in diet and extensive range, wild pigs cause extensive damage to a variety of agricultural crops throughout the U.S. Wild pigs in the U.S. are known to cause damage to grasses, cereals, vegetables, fruits, orchards, cotton, soybeans, and other crops. This extensive list has caused growing interest in better understanding the pattern and extent of agricultural damage by wild pigs (Seward et al. 2004; Boyce 2020). Research in Europe indicates that wild boar preferentially select agricultural crops over natural food resources (Herrero et al. 2006), but the seasonal availability of crops along with the presence of nutritionally dense hard mast appear to be two of the most important factors for resource selection (Fournier-Chambriollon and Fournier 1995; Massei et al. 1996; Schley and Roper 2003).

Wild pigs are a highly invasive and destructive species, so in their introduced range most management is focused on population control. Wild pig population control is usually in the form of reduction or eradication through the use of removal or exclusion programs (Ditchkoff &

Bodenchuk 2020). Removal programs, when planned right, have proven effective at reducing or eradicating wild pig populations across a broad landscape (McCann & Garcelon 2008; Parkes et al 2010). Wild pig management practices vary by state; lethal methods include shooting, dogging, toxicants, and trapping and hunting, although no toxicants are currently in use in North America to control wild pigs. Non-lethal methods include fencing, harassment, deterrents, and contraceptives, though there are no widespread contraceptives currently in use for wild pigs (Mayer and Brisbin, 2009; West et al. 2009). Hunting is one of the most popular methods of population control used, though hunting alone is not sufficient to control populations and may inversely create demand for wild pigs on a landscape (Caley & Ottely 1995; Mayer 2014). Population control methods for such a highly invasive species like wild pigs does not come cheap as to remove a single animal from the landscape costs anywhere between $18.27 and $46.95, depending on the method used (Bodenchuk 2014). Despite the extensive population control of wild pigs across their invasive range, few studies have been undertaken to understand how changes in population size result in corresponding changes in damages caused by wild pigs.

The purpose of this thesis is to better inform landowners, managers, and agencies on the impacts of control efforts on wild pig populations and their damage, and to understand the driving habitat attributes influencing where wild pig rooting behavior occurs in forested and agricultural ecosystems. In Chapter 2, I monitor wild pig populations before and during extensive removal efforts by the United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services (USDA-APHIS-WS), and document changes in environmental and agricultural damage following the implementation of population control. This was accomplished by using baited camera surveys to monitor wild pig populations, landowner surveys to gather crop damage numbers, and transect surveys to quantify environmental rooting damage. The results of Chapter 2 will provide critical data to show the effects of control efforts in reducing damages caused by wild pigs. In Chapter 3 I evaluated the habitat attributes most associated with wild pig rooting damage on both a heavily forested [i.e. Savannah River Site (SRS)], and privately owned agricultural (POA) properties in South Carolina. Transect surveys were conducted across the SRS and 17 POA to quantify rooting damage and measure local habitat attributes associated with damaged areas. The results of Chapter 3 will expand the ability of agencies, landowners, and managers to identify areas of increased impact by wild pigs and allow them to focus more resources on those areas for monitoring and removal. Collectively, this research will expand the knowledge base of all concerned about wild pigs and allow for more tailored management efforts to maximize the efficiency of limited resources.

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CHAPTER 2

CHANGES IN WILD PIG (*SUS SCROFA*) POPULATION SIZE, CROP DAMAGE, AND ENVIRONMENTAL IMPACTS IN RESPONSE TO MANAGEMENT

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Abstract

As the population and range of wild pigs (*Sus scrofa*) continue to grow across North America, there has been an increase in environmental and economic damages caused by this invasive species, and control efforts to reduce damages have increased concomitantly. Despite the expanding impacts and costs associated with management of wild pigs, the extent to which wild pig management reduces populations and diminishes environmental and agricultural damages are rarely quantified. Using a combination of wild pig population surveys, agricultural damage assessments, and environmental rooting surveys across 17 mixed forest-agricultural properties in South Carolina, USA, we quantified changes in wild pig population size and associated damages over a two-year period following implementation of a professional control program. Following implementation of control efforts, both the number of wild pig detections and estimated abundance decreased markedly. Within 18 months populations were reduced by >75%, which resulted in a corresponding decline in agricultural damage of 78% and environmental rooting by 94%. Our findings suggest that sustained wild pig control efforts can substantially reduce wild pig populations, which in turn results in reductions in crop damage and environmental rooting damage by wild pigs. Ultimately this study will help inform management strategies for controlling wild pigs and will identify thresholds at which wild pig management can reduce impacts to native ecosystems, livestock, and crops.

Key Words: Agricultural damage, environmental damage, rooting, *Sus scrofa*, wild pigs

Introduction

Invasive species can have profound impacts in areas where they are introduced, disrupting ecosystem function, creating losses and localized extinctions of native species, and negatively impacting human health and economies (Simberloff et al. 2013; Pitt et al. 2018). Wild pigs (*Sus scrofa*), which are native to Eurasia, have been introduced worldwide for food and hunting opportunities, and over the last several decades have become one of the world's most notable invasive species (Barrios-García and Ballari 2012; Mayer and Beasley 2018). Wild pigs are currently experiencing global range expansion due to translocations by humans, natural dispersal, and favorable changes in environmental conditions. Widespread accidental and intentional releases of wild pigs for the purposes of sport hunting continue across numerous countries, especially in the United States, which is believed to be the most influential driver of their population expansion today (Gipson et al. 1998; Long 2003; Bevins et al. 2014; Tabak et al. 2017; Hernández et al. 2018). In addition, expansion in the geographic distribution and abundance of wild pig populations within their native and non-native ranges has been influenced in part by human land-use and changing climatic conditions (Brook and van Beest 2014; Massei et al. 2015; Vetter et al. 2015; Frauendorf et al. 2016). Expansion of agricultural lands, in particular, can facilitate the expansion of wild pig populations through providing both cover and high-quality forage (Brook and van Beest 2014; McClure et al. 2015; Lewis et al. 2017; Snow et al. 2017).

Wild pigs are omnivorous (Ballari and Barrios-García 2014), have high reproductive rates, and low mortality due to predation, even when young (Heise-Pavlov et al. 2009; Chinn et al. 2021), which has hastened wild pig range expansion into new regions and habitats (Sales et al. 2017). In natural ecosystems, wild pigs can severely damage native habitats and sensitive ecological communities, especially riparian areas and deciduous forests (Barrios-Garcia and Ballari 2012; Hone 2012; Bevins et al. 2014). In addition, wild pigs can impact a variety of rare, threatened, and endangered species through habitat destruction, predation, and competition for resources (Barrios-Garcia and Ballari 2012). Wild pigs also host numerous parasites and diseases, many of which, like classical swine fever and *Brucella spp.* can be transmitted to other wildlife, humans, and livestock (Jay et al. 2007; Meng et al. 2009; Bevins et al. 2014; Miller et al. 2017; Corn and Yabsley 2020). These factors make wild pigs not only a successful invasive species, but also a major concern for landowners, managers, and agencies across the globe.

Within North America, wild pigs descended from escaped domestic pigs introduced nearly 500 years ago that subsequently interbred with introduced Eurasian wild boar (Keiter et al. 2016). Populations of wild pigs and associated damages remained relatively localized for centuries; however, over the last few decades the number of U.S. states and Canadian provinces reporting wild pigs has nearly doubled (Gipson et al. 1998; Bevins et al. 2014). Concurrent with this expansion, the ecological, agricultural, and economic impacts of wild pigs have increased markedly as well (Hutton et al. 2006; Mayer and Brisbin 2009; Bevins et al. 2014; Mayer and Beasley 2018). Wildlife damage to crops, in particular, is a pervasive issue affecting landowners, wildlife management agencies, and conservation organizations across the globe, and is projected to increase further if more effective population control methods are not implemented (Seward et al. 2004). Within the U.S. alone, annual agricultural damage attributed to wild pigs and associated control efforts exceeded $1.5 billion in 2007, or ~$2 billion today when adjusted for inflation (Pimentel et al. 2007). Wild pig damage to row crops is particularly extensive, both in their native and introduced range (Tack 2018; Strickland et al 2020). Corn (*Zea mays*) fields are often heavily damaged by wild pigs, but grasses, cereals, and legumes also are routinely impacted (Hererro et al. 2006; Schley et al. 2008). A landowner survey conducted in 11 southern U.S. states alone estimated annual damage to corn at over $61 million and peanuts (*Arachis hypogaea*) at over $40 million (Anderson et al. 2016).

Due to the substantive damage caused by wild pigs, populations are extensively managed throughout their invasive range, and in many U.S. states recreational hunting is a popular method of control for wild pigs. However, there is little evidence supporting the effectiveness of recreational hunting as a long-term management tool for controlling the spread of wild pigs, and in many cases sport hunting may be counterproductive to management objectives (Caley and Ottley 1995; Ditchkoff and Bodenchuk 2020). Recreational hunting typically removes ~23% of the population, on average, far below the 60-80% needed to reduce populations (Mayer 2014; Pepin et al. 2017; Ditchkoff and Bodenchuk 2020). Recreational hunting also provides financial incentives for keeping wild pigs on the landscape, which is counter to the goal of control efforts (Ditchkoff and Bodenchuk 2020). Thus, successful wild pig population control is most effectively achieved through coordinated and adaptive strategies by wildlife professionals (McCann and Garcelon 2008; Parkes et al. 2010). As a result, there are widespread and growing efforts by local, state, and federal agencies to supplement recreational hunting of wild pigs through trapping and aerial removal programs (Ditchkoff and Bodenchuk 2020).

For example, within the U.S. the Department of Agriculture established a nationally coordinated program in 2014 to mitigate damages from wild pigs to natural ecosystems, residential developments, agricultural, and rangelands (Miller et al. 2018). This program has since been supplemented through efforts by other state and federal agencies, particularly the Feral Swine Eradication and Control Pilot Program (FSCP). The FSCP was established by the 2018 Farm Bill to provide additional resources to control populations and restore lands impacted by wild pigs. Collectively, these efforts have removed vast numbers of wild pigs across the U.S. to date, successfully eliminating populations from 10 states. However, despite the extensive removal of pigs throughout the U.S. and other areas of their invasive range, and high costs associated with these efforts, there has been little effort to quantify the benefits of wild pig removal to agricultural or environmental resources. Similarly, due to limited resources for monitoring, removal efforts of invasive species typically report the number of individuals removed and rarely quantify changes in population size, which although difficult to quantify, is needed to assess the efficacy of control programs.

Therefore, our objective in this research was to quantify changes in wild pig population size and associated damages to agricultural and environmental resources in conjunction with wild pig removal efforts conducted under the FSCP, which involves extensive removal of wild pigs by professional agencies throughout several U.S. states. We predicted that professional control efforts would substantially decrease local wild pig populations resulting in corresponding decrease in both agricultural and environmental damage. These data fill critical gaps in our knowledge of the efficacy of wild pig control programs, information needed to inform and adapt management plans to reduce the impacts and spread of this highly invasive species.

Study Area

We conducted population, crop, and rooting surveys in conjunction with wild pig removal efforts conducted across 17 privately owned agricultural properties (POA properties) throughout Newberry and Hampton Counties, South Carolina, USA. Properties were mixed agricultural lands that ranged from ~66 hectares, to over ~4000 hectares in size, though their average size was ~ 600 hectares. Newberry County is in the lower Piedmont of Northcentral South Carolina and bordered by the Broad and Saluda Rivers. The Piedmont region of South

Carolina is the most inland region of the two counties surveyed and includes features such as rolling hills with stream-cut valleys and very few level floodplains. Newberry County is overwhelmingly rural, with farmland and pasture comprising approximately 53% of the total area and much of the remaining landscape composed of forested upland pine and mixed hardwoods (NASS 2020). Hampton County is located in the southwest of South Carolina in the Southern Coastal Plain, bordered on the west by the Savannah River. The Coastal Plains region features distinctive attributes such as large floodplains, river swamps, and longleaf pine (*Pinus palustris*) savannahs. Hampton County is also chiefly rural, with farmland that accounts for roughly 30% of the landscape and forested areas consisting of mostly upland pine and bottomland hardwoods making up the majority of the remainder of the county (NASS 2020). Upland pine is composed mainly of widely spaced pines with a varying shrub layer and groundcover of grasses and herbs. The canopy is dominated by loblolly pine (*Pinus taeda*) and longleaf pine, and there is a fragmented subcanopy layer of smaller pines and various hardwoods. Bottomland hardwood forests are deciduous forested wetlands made up of different species able to survive in seasonally or permanently flooded areas along bodies of water. The main canopy species include a mixture of Gum (*Nyssa sp*.), Oak (*Quercus sp*.), and Bald Cypress (*Taxodium distichum*), while the understory is composed of either dense shrubs with sparse ground cover, or open with few shrubs and a groundcover of ferns, herbs, and grasses (USGS).

Methods

<u>Wild Pig Abundance Assessments</u>

To estimate relative abundance of wild pigs on properties targeted for wild pig population control, we set baited remote camera traps (Reconyx HP2W; Reconyx, Holmen, WI, USA) throughout each property. Camera surveys were implemented immediately prior to initiation of control efforts and repeated every 6 months from January 2020 through August 2021, for a total of 2-4 surveys per site. We used ArcGIS Pro to generate random points across each property to establish camera locations, with a density of 1 camera per 25 hectares, and a minimum spacing of ~500 meters. Cameras were set to trigger on motion and programed to take 3 pictures, 1 second apart, with a 5 second quiet period between sets of pictures when triggered. Cameras were baited with 22.7 kilograms of whole corn approximately 5 meters away from the camera and left in the field for 2 weeks; cameras were re-visited on day 7 and rebaited with 11.3 kilograms of corn as necessary (Keiter et al. 2017, Schlichting et al. 2019). All images not containing wild pigs were removed before importing images into the Colorado Parks and Wildlife Photo Warehouse for detection analysis (Colorado Parks and Wildlife, Denver, CO, USA). The total number of wild pig detections for each camera on each property was quantified for each session. A detection event was classified as any time a wild pig entered the frame. If a wild pig left the frame for <30 minutes before re-entering the frame, it was still considered a single detection event. Any gaps in wild pig visits exceeding >30 minutes was considered a new detection event. Cameras were pooled for each property during each session to quantify overall detections per property, per session. Due to timing of property entry within the FSCP, while all properties were surveyed pre-control efforts, the number of post-control surveys differed. Therefore, we organized camera survey results into sessions (pre-control and 6 months, 12, months, and 18 months post initiation of control) to facilitate standardization.

Wild Pig Removal

Removal of wild pigs from properties was done by professional trappers with the United States Department of Agriculture - Animal and Plant Health Inspection Service - Wildlife Services (USDA-APHIS-WS). Upon conclusion of pre-removal wild pig abundance surveys, wild pig traps were set in preferred habitats and high pig traffic areas. Trap styles used by the USDA included corral traps, drop traps, and net traps baited with whole corn. All captured pigs were euthanized by USDA. While trapping was the main method of wild pig removal, aerial gunning by helicopter was used on one property that had large enough open areas. Initial control efforts on each property targeted large groups of wild pigs and were sustained until targeted pigs were captured, after which properties were monitored by remote cameras (see above) or anecdotally through landowners and trapping was reinitiated or maintained accordingly. USDA documented all removals, including property, date, time, age class (e.g., juvenile or adult) of removed animals, trap type, and sex.

Agricultural Damage Surveys

Agricultural damage assessments were conducted for all 17 properties involved in this study using in-person and telephone surveys. Landowners signed up through the removal program were contacted prior to control efforts to gather pre-control crop damage data, and again roughly one year later to reassess crop damage after control efforts were implemented. Trained surveyors used a standardized questionnaire for each property. The questionnaire included total crop area for any crop types present on the property, total crop damage, total crop damage due to wild pigs, total area replanted, total crop conversions due to wild pig damage, and total monetary and time losses due to wild pig damage. We used landowner responses from these surveys to estimate crop damage caused by wild pigs (hectares) for the year prior to initiation of wild pig control and one year post removal (Tzilkowski et al. 2002). Damage not associated with wild pigs was excluded. Crop damage surveys were conducted with Institutional Review Board (Project:00002907) approval through the University of Georgia.

Environmental Damage Surveys

To quantify changes in environment rooting damages attributed to wild pigs, we conducted systematic rooting damage surveys on all 17 properties. Within each property, we established 10 randomly placed transects spaced a minimum of ~50-100 meters apart, and the length of transects was determined such that 1% of the total natural area (total property area – crop area and developed area) of each property would be surveyed across the 10, 10 meter wide transects. Randomization of transects was performed by using ArcGIS Pro to establish 10 random points within each property, which were used as starting points for each transect, and then a random number generator was used to establish an azimuth for each of the 10 transects. Transects were walked by trained observers who recorded the presence, intensity (depth in centimeters), and area (square meters) of the transect impacted by rooting. Transects were georeferenced with a GPS and surveyed once prior to control efforts, and again one year later, following the implementation of wild pig control. Due to timing of sign-up, one property was only surveyed prior to control efforts, but was not surveyed again before the end of the study, and thus was excluded from our environmental damage analysis. A standardized aging structure was used to classify damage into one of 3 age groups: 1) damage approximately ~0-1 months old characterized by rooting damage where plants had been destroyed and regrowth had not happened yet, and no or little debris had fallen into the damage area, 2) damage ~1-6 months old, which included damage where new plant regeneration was present in the damaged area but there was no or little debris covering the damage, and 3) ~6+ months old damage, which included rooting that had plant regeneration and was mostly covered with debris. Any damage located within the 10 meter wide transect and classified into age groups one or two was used in our analysis.

Statistical Analysis

We estimated wild pig abundance for each property using two approaches. First, we developed a relative abundance index of detections per camera hour. Camera hours were calculated for each property by multiplying the number of cameras by the number of hours each camera was deployed. The number of detections for each site was then divided by the total camera hours and multiplied by 100. This was conducted for each session to provide an average relative abundance index for each property during each session (pre-control, 6 months, 12 months, 18 months). In addition to the relative abundance index, for 10 of the 17 properties we had sufficient detections across our 4 sampling periods to estimate abundance using binomial n-mixture models. N -mixture models use data from repeated surveys of multiple sites (cameras) within a period of population closure to estimate detection probability of individuals, which produces an estimate of population abundance (Royle 2004). We used the pcount function of unmarked in the program R to fit our n-mixture models, which transforms the data. Using the pcount function, detection count data for each camera was used to calculate detection probability and wild pig abundance for individual cameras; the model was then back-transformed using the backtransform function. Using the predict function, camera site detection probability and abundance estimates were used to estimate property level abundance for each session (pre-control, 6 months, 12 months, 18 months). Normality of the both relative abundance indexes and n-mixture model abundances were tested using a Shapiro-Wilk test. Due to the non-normality of the data, we then conducted separate Wilcoxon signed rank tests to test for differences in estimated relative abundance between pre control and the last survey performed on each property.

We compiled agricultural damage and environmental damage recorded for all properties for each year (2019, 2020) and tested these datasets for normality using a Shapiro-Wilk test. Due to non-normality of our data, we then conducted separate exact Wilcoxon signed rank tests to test for differences in agricultural and environmental damage between years. All statistical analyses were performed in R version 1.3.1073, and the significance level was determined by $p < 0.05$.

Results

Wild pig removal by the USDA-APHIS-WS during the program ranged from 0-124 individuals per property. USDA removed a total of 302 wild pigs from 17 properties during 2020 (~7.92 ±3.18 SE), and 281 wild pigs during 2021 (~3.38 ±0.99 SE) (Figure 2.3). Of the wild pigs removed in 2020, ~22% were adult males, ~26% were adult females, ~26% were juvenile males, and ~26% were juvenile females. The wild pigs removed in 2021 consisted of 21% adult males, 25% adult females, 25% juvenile males, and 29% juvenile females.

Over the two years of this study, 534 cameras were deployed to survey the 17 properties, resulting in 7476 total camera nights. Due to the timing of landowner participation, all properties were surveyed at least twice, once before control efforts and once ~6 months later. Fifteen properties were surveyed at least three times (pre-control, ~6 months, 12 months, 18 months), and eight were surveyed four times over the 18 months. Relative abundance indexes showed that average detections per camera hour significantly declined ~76% ($p=0.013$) from 69.95 (±20.9 SE) per property during our pre-control survey to 16.73 (±5.7 SE) per property following implementation of population control (Figure 2.1). Similarly, N-mixture models for estimated abundance dropped on average 81% ($p= 0.447$) from 69.61 (±36.9 SE) individuals per property during our pre-control survey to 13.16 (±3.8 SE) individuals estimated per property over the same time period (Figure 2.2).

All property owners were surveyed and crop damage was estimated based on landowners' responses before control efforts began and again one year later. One property was excluded from analyses because it did not include any agricultural land. All other property owners reported agricultural damage associated with wild pigs. Damage reported by landowners varied greatly between our two survey periods. During pre-control surveys reported damage from wild pigs ranged from 0-25.5 ha, while after control reported damage ranged from 0-3.6 ha. Overall agricultural damage estimated from landowner surveys significantly decreased following implementation of control ($p=0.028$), declining on average by 78% from 5.28 ha (±1.9 SE) to 1.18 ha (±0.34 SE) per property (Figure 2.6).

Environmental rooting damage was found on all but two properties prior to control, whereas no environmental damage was found on nine properties after control. Following the implementation of wild pig control, rooting damage by wild pigs decreased markedly ($p=0.003$). Environmental rooting damage ranged from 0-1552 m^2 before control efforts to 0-285 m^2 one year after control. Prior to control, we recorded an average of 370.28 m^2 (±122.6 SE) of rooting damage per property across our damage transects. One year into removal efforts environmental damage was reduced by 94%, averaging 21.24 m^2 per property across our damage transects (±16.6 SE) (Figure 2.7).

Discussion

Despite extensive control programs to reduce populations of wild pigs across much of their invasive range, efforts are rarely undertaken to quantify the efficacy of removal programs at mitigating impacts. Here we present results of a study quantifying changes in the abundance of wild pigs following the implementation of an adaptive control program, and the impact of changes in wild pig density on the extent of agricultural and environmental damage across private mixed agricultural and forested lands. Although numbers of wild pigs removed was similar between years, our results revealed control efforts were successful in reducing the abundance of wild pigs on private agricultural lands by over 75%. These population reductions were found to directly influence the extent of damages caused by wild pigs, as agricultural damage from wild pigs decreased by 78% and environmental rooting damage decreased by 94% within one year of the implementation of population control measures. These findings are consistent with a previous study that found that intensive trapping efforts can mitigate damage to rangelands by wild pigs (Gaskamp et al. 2018) and suggest wild pig control efforts that implement extensive and adaptive trapping approaches can be an effective management tool for reducing populations and ultimately reducing damage associated with wild pigs.

Wild pigs are ecological generalists with high reproductive capabilities and low mortality, which allows them to not only expand into new habitats but also increase populations quickly in response to management or population introductions (Mayer and Brisbin 2009; Servanty et al. 2011; Chinn 2021). As a result, it is difficult for managers to control populations of wild pigs once they have become established within a landscape. Indeed, populations of wild pigs have continued to increase throughout much of their invasive range over the last few decades, despite their popularity as a game species and extensive control programs (Mayer 2014). Due to their high fecundity, an estimated 60-80% of the wild pig population needs to be removed annually to control populations (Mayer 2014). While recreational hunting is generally one of the most popular population management methods for wildlife, hunting alone has been demonstrated to be insufficient for controlling wild pig populations, and alternative or supplementary approaches such as trapping are needed to achieve management goals (Ditchkoff & Bodenchuk 2020). Trapping can be particularly effective for removing animals that form social groups like wild pigs (Choquenot et al. 1993) and there is increased recognition that targeting trapping that systematically removes entire social groups may be most effective for controlling wild pig populations (Sparklin et al. 2009). Indeed, control programs implemented in our study targeting social groups were able to reduce populations by approximately 80%, on average. This falls into the documented range needed to achieve negative growth rates in wild pig populations and suggests sustained adaptive trapping programs can be effective in controlling populations over relatively short timeframes. However, further studies are needed to determine the long-term efficacy and costs associated with sustained wild pig management programs. In addition to trapping, aerial shooting is becoming an increasingly effective and cost-efficient means of removing wild pigs (Bodenchuk 2014), and other methods of population control such as toxicants are under development. Thus, although our results demonstrate trapping alone targeting entire social groups can effectively manage wild pigs, future studies should evaluate the extent to which integration of other management approaches such as aerial shooting can accelerate population reduction and minimize costs.

Agricultural damage such as direct consumption, trampling, and rooting caused by wild pigs is a widespread problem for producers and managers. Wild pigs have highly variable diets and are known to cause damage to a variety of crops, including grasses, cereals, vegetables and fruits, orchards, cotton, and soybeans (Seward et al. 2004; Barrios-Garcia & Ballari 2012; Ballari & Barrios-Garcia 2013). Within 11 states in the southern U.S. alone, annual damage to corn (*Zea mays*) and peanuts (*Arachis hypogaea*) from wild pigs has been estimated at over $101 million (Anderson et al. 2016). Similarly, within their native range wild boar cause extensive damage; in Poland, $13.4 million worth of compensation for wild boar damages was given out to farmers in 2010 (Frackowiak et al., 2012). Following the implementation of control efforts in our study, reported agricultural damage associated with wild pigs fell on average 78%, suggesting management of wild pigs can substantially reduce crop losses to producers. Further reductions in crop damage could be achieved through focused removal efforts immediately prior to peak periods of crop depredation by wild pigs. For example, Boyce et al. (2020) found wild pigs commonly consumed crops such as corn and peanuts soon after planting, with further damage to corn during later stages of development. These links are important for landowners and managers in deciding when it is best to implement control efforts to save on limited resources.

Wild pigs also are known to cause extensive environmental damage with their rooting and wallowing behavior, yet few studies have characterized impacts of wild pig rooting to native ecosystems. Wetlands are known to be heavily selected for by wild pigs due to their ample food, cover, and water resources (Clontz et al 2021). However, wetlands are sensitive ecosystems, often containing threatened and endangered species that can be disrupted by rooting and wallowing (Engeman et al. 2004, West et al 2009). In our study, rooting damage by wild pigs was found across almost all study sites, with as much as 1552 m^2 of rooting damage recorded within a single property. Further, rooting damage was concentrated mainly around resources such as wetlands and crops, highlighting the potential impacts of wild pigs to wetland habitats (Chapter 3). Similar to crop damage surveys, we observed a substantial decrease (94%) of wild pig rooting damage after the implementation of control efforts, and nine sites had no damage on our transects after one year. Given that our surveys were limited to 1% of the natural area of each site (total area – developed and crop area), it is likely these sites still sustained some rooting damage by wild pigs after initiation of control efforts. Nonetheless, these results suggest changes in damage caused by wild pigs is closely linked to changes in population size, and thus benefits achieved through removal programs can be estimated through establishment of population monitoring programs.

Collectively, our results demonstrate extensive trapping programs can be highly successful in not only removing large portions of wild pig populations off the landscape, but also in reducing agricultural damage and environmental damage. Thus, investments in wild pig management programs can be effective in reducing economic and environmental impacts of wild pigs, and should be associated with monitoring programs to inform adaptive approaches to maximize the efficacy of management investments. Although our study focused only on properties where population control programs were implemented, there are likely additional benefits to the surrounding landscape. Within fragmented agricultural landscapes wild pig home ranges often extend across multiple property boundaries. Therefore, for many of our study sites wild pigs likely were removed that incorporated adjacent properties within their home range boundaries. As a result, in landscapes with fragmented ownership control efforts implemented on one property may have broader impacts through reducing damage on adjacent properties as well (Gaskamp et al. 2018). Thus, while individual landowners may not have the resources for intensive removal efforts, groups of landowners may be able to share resources to reduce damage from wild pigs across more extensive areas. However, without widespread participation from private landowners, areas that can be used by wild pigs as safe havens will continue to limit the efficacy of control programs. This study only monitored properties for ~18 months, so more long-term studies are needed to determine the long-term efficacy of wild pig management programs, particularly after management by state and federal agencies ceases and is maintained by local landowners. More research also should be undertaken to quantify benefits of wild pig removal efforts to surrounding landowners. In addition, research into the efficiency and cost of varied management approaches would help further tailor management efforts that are constrained by limited resources.

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Tables and Figures

Table 2.1. Property area, number of wild pigs (*Sus scrofa*) removed, pre and post control wild pig relative abundance index (RAI), pre and post control wild pig n-mixture model abundance, pre and 12 months into control agricultural damage attributed to wild pigs, pre and 12 months into control environmental damage by wild pigs for 17 properties in South Carolina, USA.

Property ID	Area (ha)	Wild Pigs Removed 2020	Wild Pigs Removed 2021	Pre-control RAI	Post-control RAI	Pre-control N-mix	Post-control N-mix	Pre-control Ag. Damage (ha)	12 months Ag. Damage (ha)	Pre-control Env. Damage (m^2)	12 months Env. Damage (m^2)
MK1	327.9	36	39	41	24	N/A	15.42	0	0	442	0
SW1	85.2	0	1	0	4.8	0	1	9.5	0	22	0
SW2	356.9	0	0	0	0	0	0	2.5	0	376	0
S1	338.4	0	0	0	16	0	1.25	50	0.5	1	0
Y2	216.4	14	0	0	0	0	0	24.2	0	52	0
Y1	611.1	51	31	58	11	246.63	12.401	62.99	1	1552	285
LSP1	232.4	12	9	16	43	16.09	22.35	0	1	861	3
TB1	50.3	25	6	314	3.5	N/A	N/A	4	0.5	922	N/A
WC1	573.8	25	21	74	29	49	53.87	13	11	560	4
B1	50.5	15	0	93	54	N/A	N/A	3.5	4.5	0	0
ISE1	314.8	14	0	67	38	54.52	54.05	0	9	100	0
W1	46.7	6	0	207	46	N/A	N/A	4	3	0.25	5
BO1	258.6	0	0	1.2	0	0	0	4	4	10	6
BO2	349.8	0	15	49	3.9	56.38	19.24	4	4	73	0
CL1	3921	104	124	128	17	322.5	44.87	37	8	1323	12
H&B1	584.9	0	19	8	36	N/A	N/A	3	2	0.5	20
D1	175.2	0	16	133	4.5	N/A	2.25	0	1	26	N/A

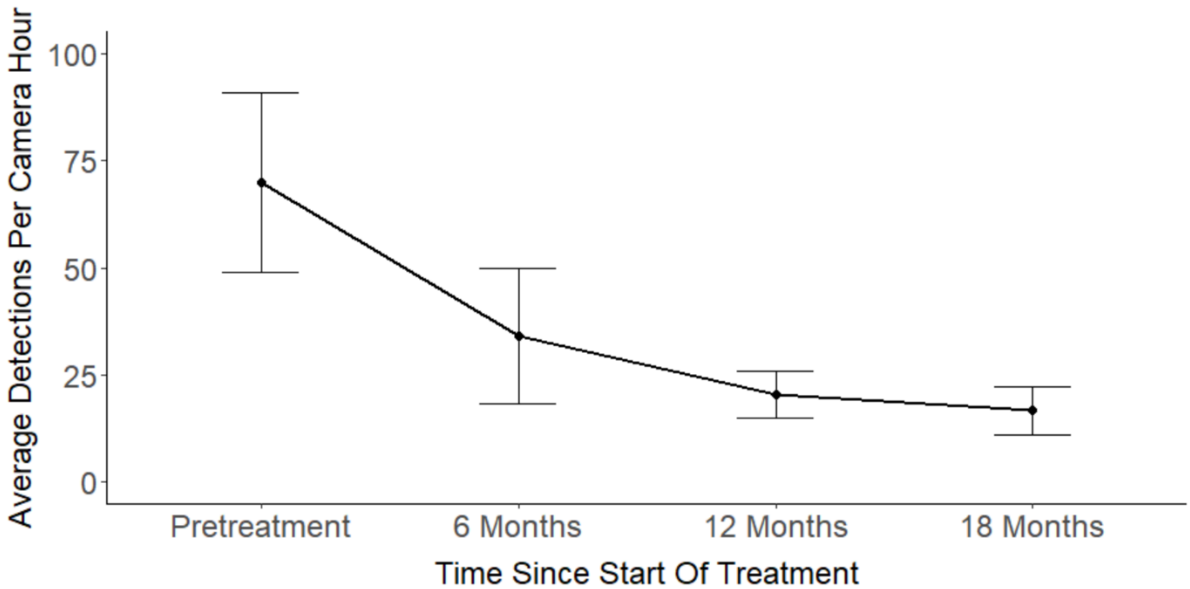

Figure 2.1. Average estimates with standard errors from a relative abundance index for wild pigs (*Sus scrofa*) on 17 properties in South Carolina, USA, 2020-2021.

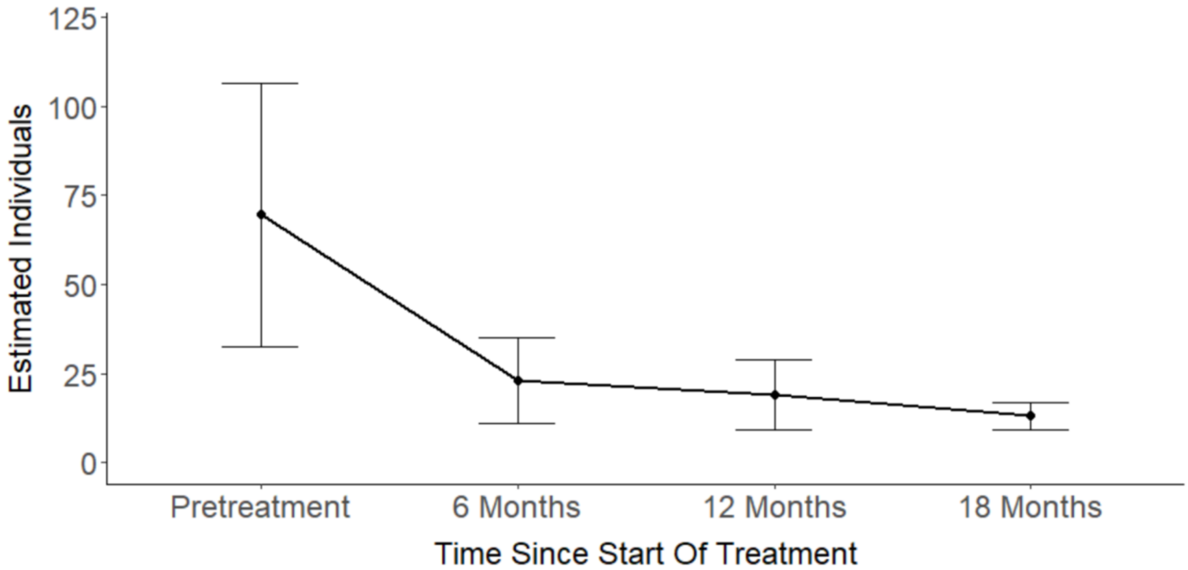

Figure 2.2. Average abundance estimates with standard errors from an N-mixture model for wild pigs (*Sus scrofa*) on 17 properties in South Carolina, USA, 2020-2021.

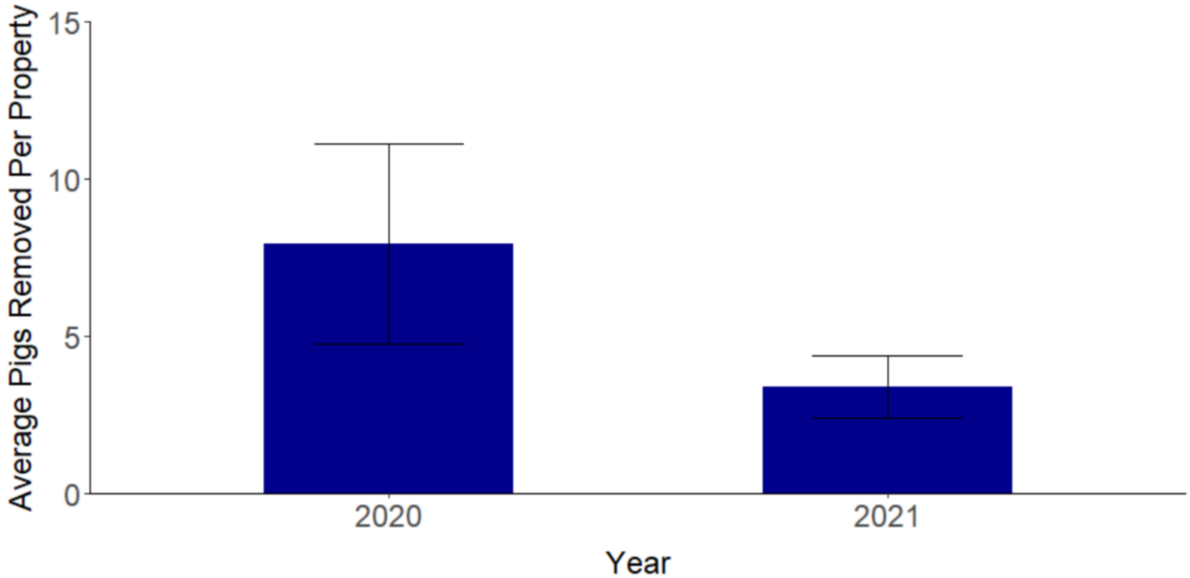

Figure 2.3. Wild pigs (*Sus scrofa*) removed per property, standardized by property size (km^2), with standard error bars for 17 properties in 2020 and 2021 in South Carolina, USA.

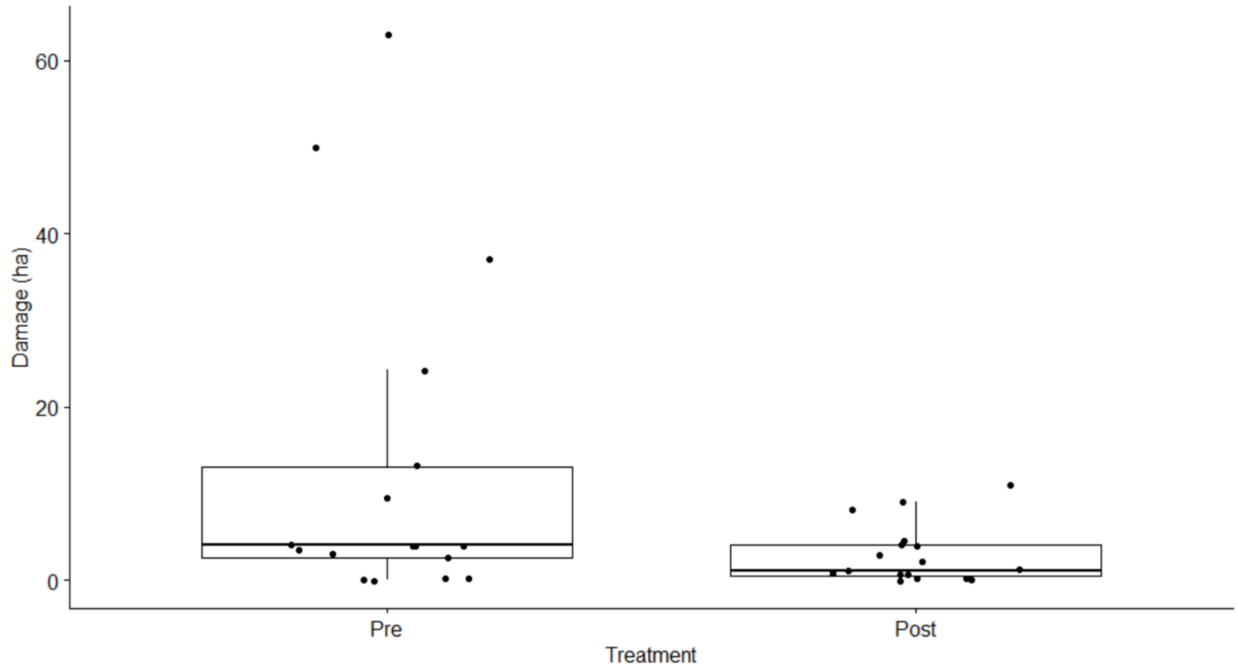

Figure 2.4. Landowner reported crop damage estimates caused by wild pigs (*Sus scrofa*) across 17 privately owned agricultural properties (POA) in South Carolina, USA prior to (2019) and one year post initiation of removal efforts (2020).

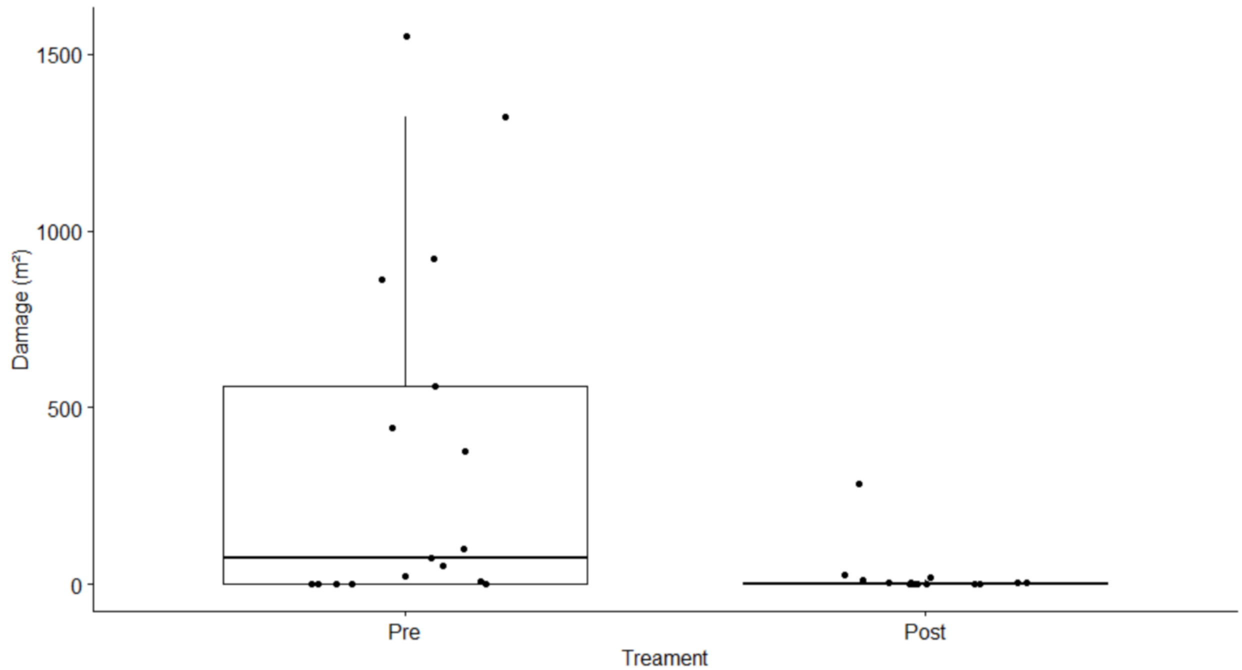

Figure 2.5. Environmental rooting damage caused by wild pigs (*Sus scrofa*) across 17 privately owned agricultural properties (POA) in South Carolina, USA prior to (2020) and one year post initiation of removal efforts (2021).

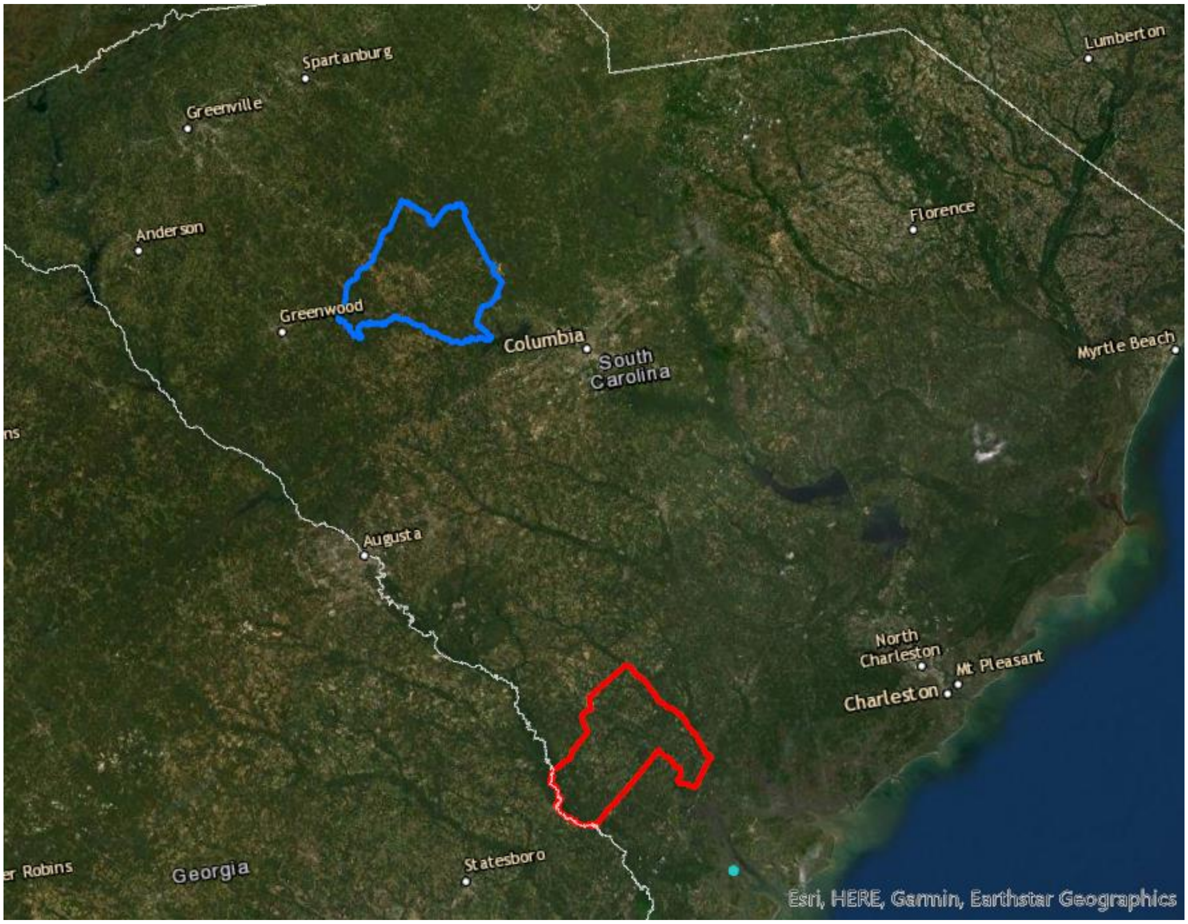

Figure 2.6. Map of South Carolina, USA, showing (Red) Hampton County, and (Blue) Newberry County.

Figure 2.7. Environmental and agricultural damage caused by wild pigs (*Sus scrofa*) from 17 privately owned agricultural properties (POA) in South Carolina, USA.

CHAPTER 3

INFLUENCE OF HABITAT ATTRIBUTES ON THE DISTRIBUTION OF WILD PIG (*SUS SCROFA*) ROOTING DAMAGE IN FORESTED AND AGRICULTURAL ECOSYSTEMS

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Abstract

The rapid expansion of wild pig (*Sus scrofa*) populations over the last few decades has resulted in an increased distribution of damages to native ecosystems throughout their introduced range. Despite the extent of wild pig damage and the growing concern from land managers, there is little data regarding the variability of damage in relation to season and habitat attributes. In this study we assessed wild pig rooting damage in two seasons along 52 km of transects throughout primarily forested and mixed forest-agricultural ecosystems in South Carolina, USA. We recorded fine-scale habitat attributes at damage and control sites to determine habitat attributes most closely associated with wild pig rooting damage in each landscape. Within predominantly forested ecosystems, damage was most extensive during winter and wild pigs selected for presence of mast trees for rooting. Our modelling results also suggested wild pigs selected for hardwood stands and areas proximal to water sources for rooting but showed an avoidance of areas with higher tree density and areas closer to roads. Similarly, within mixed forest-agricultural ecosystems, wild pigs selected for areas with lower tree density and farther from roads, but closer to crops. Our results demonstrate that wild pigs exhibit preferences in resource selection associated with rooting that can help facilitate increased efficiency of management. These results will also help with early detection of wild pig expansion by highlighting key areas to monitor for wild pig presence.

Key Words: Invasive, resource selection model, rooting, *Sus scrofa*, wild pigs

Introduction

Wild pigs (*Sus scrofa*) are a globally distributed species that are both a popular game animal but also cause extensive ecological, economic, and agricultural impacts to natural and anthropogenic ecosystems throughout both their native and invasive ranges (Mayer and Beasley

2018; VerCauteren et al. 2020). Within the U.S. alone damage and control costs associated with invasive wild pigs are estimated to exceed 1.5 billion dollars annually (Pimentel 2007). Further, concerns over the potential disease risks wild pigs pose, particularly transboundary animal diseases such as African Swine Fever and Classical Swine Fever, which pose an economic risk to domestic producers (Meng et al. 2009; Cleveland et al. 2017), has spurred governmental action and increased multi-disciplinary interest in expanding management efforts of this species. However, despite the growing interest in controlling populations to mitigate environmental and economic impacts, many aspects of wild pig ecology, impacts, and management needed to inform adaptive management approaches remain understudied (Beasley et al. 2018).

Domestic pigs first appeared in North America in the 1500s where they established feral populations and over time interbred with escaped or released European wild boar (Mayer and Beasley 2018). As a result, wild pigs throughout much of North America today have mixed genetic ancestry (Keiter et al 2016; Smyser et al 2020), with characteristics of domestic and wild populations that have facilitated their survival across diverse habitats and climates. Although populations remained relatively stable until the late 1990s, their distribution has increased explosively over the last few decades (Snow et al. 2017; Mayer and Beasley 2018). Today, wild pigs are one of the most abundant and widespread invasive vertebrates in the U.S., with an estimated 6.4 million individuals and established populations in at least 38 states (Seward et al. 2004; Bevins et al. 2014; Snow et al. 2017; Mayer and Beasley 2018; Lewis et al. 2019). Concurrently, over the last few decades wild boar numbers have increased within their natural range in Eurasia as well as in other parts of their non-native range such as Australia and South America with similar detrimental impacts (Froese et al. 2017; Iacolina et al. 2018; McDonough, 2022).

The rapid and widespread growth of wild pig and wild boar populations globally has placed a burden on local, state, and federal management agencies (Mayer and Brisbin 2009; Grady et al. 2019). However, wild pigs are extremely difficult to manage due to their adaptability and high reproductive capacity (Keiter and Beasley 2017; Chinn et al. 2021). Indeed, wild pigs throughout their introduced range have the largest reproductive potential of any large, free-ranging mammal and under favorable conditions females can reproduce year-round (Mayer and Brisbin 2009; Taylor et al. 1998; VerCauteren et al. 2020). This high reproductive rate is especially problematic as there are few or no predators of adult wild pigs throughout much of their invasive range, and juvenile survival is relatively high, especially after a few weeks of age (Keiter et al. 2017; Chinn et al. 2021). As a result, harvesting by humans is generally the leading cause of mortality among monitored wild pig populations (Gabor et al. 1999; Hanson et al. 2009; Hayes et al. 2009; Servanty et al. 2011).

Wild pigs are ecological generalists, which allows them to adapt quickly to new habitats and outcompete native species (McDonough et al. 2022). Studies on the diets of wild pigs have found that plants make up a large portion of the material consumed and is supplemented by invertebrate and vertebrate animals obtained through scavenging and predation (Robeson et al. 2017; Turner et al. 2017; Ditchkoff and Mayer 2009). Wild boar and wild pigs extensively use agricultural crops when available (Herrero et al. 2006; Boyce et al. 2021) but may preferentially select non-agricultural food resources when abundant (Wilber et al. 2019). Thus, the seasonal availability of crops along with the presence of nutritionally dense hard mast appear to be two of the most important factors influencing resource selection (Fournier-Chambriollon and Fournier 1995; Massei et al. 1996; Schley and Roper 2003). Moreover, wild pigs are adapted to take reproductive advantage of pulses in food availability, such as hard mast (Loggins et al. 2002), through increased reproduction and survival rates (Bieber and Ruf 2005).

Wild pigs cause extensive damage to native ecosystems and agriculture through their foraging behavior, called rooting, where they overturn soil in search of plant matter, insects, and other food items (Bankovich et al. 2016). Wild pigs are considered ecosystem engineers for the role they play in shaping habitat through rooting (Boughton and Boughton 2014). While rooting damage in agricultural systems is now the subject of much research, disruption of soil in natural systems has received far less attention. Rooting damage by wild pigs decreases vegetation cover, which can lead to soil erosion, alteration of soil properties and layering, and damages the soil microbiome (Barrios-Garcia and Ballari 2012). In addition, wild pigs are documented to negatively affect water quality, which can impact sensitive native aquatic species and irreparably harm fragile wetland and aquatic ecosystems (Brooks et al. 2020; Bolds et al. 2022).

The movement behavior of wild pigs is driven largely by variation in the distribution of resources such as cover, forage, and water sources throughout the landscape (Gray et al. 2020). Movement studies have indicated seasonal availability of forage, vegetation cover, and other landscape features such as proximity to water determine habitat use, with wild pigs largely selecting for bottomland hardwood or similar wetland and riparian habitats, as well as areas with extensive canopy cover (McClure et al. 2015; Clontz et al. 2021). Wild pig rooting studies have generally found similar trends between habitat selection and changes in wild pig foraging locations, both being driven by the abundance and availability of more preferred foods such as fruits, seeds, and grains, while roots and bulbs are taken secondarily when other foods are unavailable (Welander 2000). Wild pigs generally root more frequently in deciduous forests and woody wetlands; however, fine scale habitat attributes influencing rooting behavior of wild pigs such as tree density, hard mast presence, understory density, and ground cover vegetation aren't well studied (Bratton et al. 1982; Beasley et al. 2018; Gray et al. 2020; Ferretti et al. 2021).

In general, environmental damage is the least studied and most difficult impact of wild pigs to quantify. Studies attempting to ascertain the total environmental impact of wild pigs found a lack of sufficient quantification of damage to native plant and animal communities (Massei and Genov 2004). This lack of data is due to a multitude of factors, including difficulty in measuring certain environmental damages such as species loss, alteration of soil, and decreased water quality, and the objectivity in placing a value on those attributes. The objective of this study, therefore, was to quantify seasonal changes and fine-scale habitat attributes associated with wild pig rooting damage to forested ecosystems in the Southeastern U.S. These data are needed to elucidate fine-scale spatial and temporal characteristics associated with wild pig damage to guide management for reducing impacts of wild pigs to native ecosystems. We predicted wild pig damage would be most prevalent during the winter season, and given their extensive use of riparian areas, damage would be most associated with wetlands, hardwood areas, and agricultural boundaries.

Study Area

Much of this study was carried out at the Savannah River Site (SRS), a U.S. Department of Energy (DOE) facility that borders the Savannah River near Aiken, South Carolina. The SRS is in the Sandhills region, which is characterized by rolling hills capped by sands, located between the Piedmont and Coastal Plains. The SRS is approximately 800 km^2 with much of the habitat comprised of upland pine and bottomland hardwood habitat (Clontz et al. 2021). Upland pine is composed mainly of widely spaced pines with a varying shrub layer and groundcover of grasses and herbs. The canopy is dominated by loblolly pine (*Pinus taeda*) and longleaf pine

(*Pinus palustris*), and there is a fragmented subcanopy layer of smaller pines and various hardwoods. Bottomland hardwood forests are deciduous forested wetlands made up of different species able to survive in seasonally or permanently flooded areas along bodies of water. The main canopy species include a mixture of Gum (*Nyssa sp*.), Oak (*Quercus sp*.), and Bald Cypress (*Taxodium distichum*), while the understory is composed of either dense shrubs with sparse ground cover, or open with few shrubs and a groundcover of ferns, herbs, and grasses (USGS). Before the site was purchased by the DOE, wild pigs had already been established and concentrated along the river swamp of the Savannah River (Mayer et. al 2020). Despite management efforts since the late 1950's, the distribution of wild pigs over the last few decades has expanded, and they now occupy all habitat types across the SRS in high densities (Keiter et al. 2017).

In addition to the SRS, we also conducted rooting surveys across 17 privately owned agricultural properties (POA properties) throughout Newberry and Hampton Counties, South Carolina, USA. Properties were mixed agricultural lands that ranged from ~66 hectares to over ~4000 hectares in size, though the average size was ~ 600 hectares. Newberry County is in the lower Piedmont of Northcentral South Carolina and bordered by the Broad and Saluda Rivers. The Piedmont region of South Carolina is the most inland region of the three surveyed and includes features such as rolling hills with stream-cut valleys and very few level floodplains. Newberry County is overwhelmingly rural, with farmland and pasture comprising approximately 53% of the total area and much of the remaining landscape composed of forested upland pine and mixed hardwoods (NASS 2020). Hampton County is located in the southwest of South Carolina in the Southern Coastal Plain, bordered on the west by the Savannah River. The Coastal Plain region features distinctive attributes such as large floodplains, river swamps, and longleaf pine savannahs. Hampton County is also chiefly rural, with farmland that accounts for roughly 30% of the landscape and forested areas consisting of mostly upland pine and bottomland hardwoods making up most of the remainder of the county (NASS 2020).

Methods

To quantify differences in damages attributed to wild pigs in relation to season and habitat attributes, we conducted systematic rooting surveys on the SRS. Damage surveys on the SRS were conducted during both winter and summer of 2020. Nine square grids, each 200 hectares in area, were randomly placed on the SRS using ArcGIS Pro to randomly generate nine points on the SRS, which were used as the center for each grid. Grids were spaced at a minimum distance of one kilometer and avoided large water features. Within each grid, 10 transects spaced ~50-100 meters apart and ~202 meters in length were established and all damage was recorded within five meters of either side of each transect. The length of transects was determined such that 1% of the total natural area of each grid would be surveyed across the 10, 10 meter wide transects.

At the starting point of each transect, vegetation data was recorded as a control point, and subsequent vegetation data was sampled at each damage site along the transect. Three concentric circles were used for vegetation data collection; this included a one-meter diameter circle, a five-meter diameter circle, and a 15-meter diameter circle. At sampled damage sites, the center point of all three concentric circles was positioned one meter away from the edge of the damage, so that damage would not interfere with the one meter vegetation circle. Within the one-meter quadrant circle, the estimated percentage cover was recorded for each of seven ground cover designations: forbs, vine, woody, fern, grass, bare, and litter. The five-meter circle plot was used as a woody stem count for any woody stem less than 10.16 centimeters diameter at breast height

(DBH), and the dominant understory species was recorded. Within the 15-meter circle plot, all trees with >10.16 centimeter DBH were recorded and grouped into four categories: midstory pine, overstory pine, midstory hardwoods, and overstory hardwoods. Hard mast trees present in the 15-meter circle were noted, specifying whether they were oaks or other mast species. Transects were walked by trained observers who recorded the presence, intensity (depth in centimeters), and area (square meters) of the transect impacted by rooting, as well as vegetation data including understory cover, woody vegetation stem count, and tree density. Transects were georeferenced with a GPS and surveyed once during winter 2020, and again during summer 2020 to quantify changes in rooting damage in relation to habitat characteristics between seasons. A standardized aging structure was used to classify damage into one of 3 age groups: 1) damage approximately ~0-1 months old characterized by rooting damage where plants had been destroyed but regrowth had not happened yet, and no, or little debris had fallen into the damaged area, 2) damage ~1-6 months old, which included damage where new plant regeneration was present in the damaged area but there was no or little debris covering the damage, and 3) ~6+ months old damage, which included rooting that had plant regeneration and was mostly covered with debris. Any damage located within the 10 meter wide transect was classified during the first survey, and during the second survey we only recorded damage that was incurred since the previous survey (i.e. damage classifications one and two). We used publicly available GIS layers (National Wetlands Inventory, South Carolina Department of Transportation, National Land Cover Database) to delineate crops, forest type, roads, and water sources and calculated straight line distance to roads, crops and water, as well as forest type for each damage and control point in ArcGIS Pro. Forest types were then condensed into hardwoods or evergreen for analysis.

To supplement our data from SRS, systematic rooting damage surveys were also conducted throughout 17 POA properties across two South Carolina counties to further evaluate the effects of habitat attributes on wild pig rooting behavior. These additional sites were surveyed to quantify habitat attributes correlated with wild pig rooting within a more fragmented, agricultural ecosystem. These properties were only surveyed during a single season in 2020 (i.e., winter or summer), with ten of the properties surveyed in winter and seven in summer. All surveys were conducted pre-control efforts on POA properties. POA survey methods were identical to those described above for the SRS with the addition of including distance to crops, which were excluded from the SRS data due to the absence of crops in that landscape.

Statistical Analysis

We modeled habitat damage following a use–availability design, where damage sites were "used", and control sites were "available". We modeled the influence of nine environmental covariates and season (Table 3.1) on the presence (response variable) of rooting damage for our SRS dataset; POA property data were analyzed separately using the same approach apart from including crops as a fixed effect and a random variable accounting for season. Only damage included in the age classification groups 1 and 2 (i.e., <6 months) were included in the statistical analysis to ensure a consistent evaluation period for our two study periods. The variable 'ID' was included as a random effect to account for individual grids (SRS) and properties (POA) in the models and all other variables included as fixed effects. We fitted a Generalized Linear Mixed-Effect Model (GLMM) using a Gaussian distribution (Bolker et al. 2008) with a "null" model (response and random effect variable), a "master" model including all fixed and random effects, and for the SRS surveys a nested "season:master" model (SRS data only) including seasonal interactions with all fixed effects. We then developed 20 subsequent models (Table 3.2) for the SRS and 19 models (Table 3.3) for the POA properties using combinations of variables grouped based on literature of wild pig habits and preferences to determine their influence on habitat attributes associated with wild pig rooting damage. We ranked models using Akaike Information Criterion (AIC) (Burnham and Anderson 2002), and models within Δ2 AIC of the top model were considered supported. Odds ratios for each habitat attribute included in the top model were graphed with profile likelihood 95% confidence intervals. All statistical analyses were performed in R version 1.3.1073 using the packages 'lme4′ for fitting GLMM. The significance level was set at $p < 0.05$.

Results

Over the course of two seasons in 2020 we conducted 180 rooting damage surveys on the SRS. During the winter we conducted 90 transect surveys and characterized habitat attributes associated with 61 damage locations and 90 control locations. Subsequently, during the summer we resurveyed the same 90 transects and characterized 31 damage locations along with 90 control locations. Wild pig damage recorded during the ~20 kilometers surveyed totaled an area of 3765.03 m^2, with an average rooted area of 24.8 m^2, and an average depth of 12.16 cm per damage site during the winter session. The summer session had 3060.5 m^2 of damage, with an average area of 24.5 m^2, and an average depth of 11.32 cm per damage site. Across the 17 POA properties, we conducted a total of 170 rooting damage surveys during 2020. During the winter we conducted 100 transect surveys totaling ~16 kilometers and characterized habitat attributes associated with 67 damage locations. Subsequently, during the summer we surveyed 70 transects, also totaling ~16 kilometers, and characterized 37 damage locations. Across these transects we recorded a total damaged area of 4787.3 m^2, with an average area of 71.45 m^2, and average depth of 11.81 cm per damage site during the winter session. During the summer session we recorded 1506.5 m^2 of damage, with an average area of 40.72 m^2, and average depth of 10.47 cm per damage site.

Our modeling results for the SRS produced a single top model; the next closest model was 4.07 (ΔAIC) from the top model, so no other models were considered supported (Table 3.2). The top model had a weight of 0.81 and included season as a fixed effect (not nested), forest type, distance to water, distance to roads, tree density, and mast tree presence (Table 3.2). On the SRS, there was an increased likelihood of wild pigs rooting in areas farther from roads, a decreased likelihood in selection for increased tree density, and an increased likelihood of selecting for areas closer to water, all of which were non-significant. In addition, more wild pig rooting was detected in winter, as well as increased rooting in the presence of mast trees and in hardwood habitat, with both mast tree presence and season being important variables in the model (Figure 3.1).

Our modeling results for the surveys conducted on the POA properties produced two competitive models (Table 3.3). The top model had a weight of 0.32 and included distance to roads and tree density (Table 3.3). Similar to the models for the SRS, the top model for the POA properties showed an increased likelihood of selecting for areas farther from roads for rooting and decreased rooting in areas with increased tree density, with tree density being most influential (Figure 3.2). In addition to these variables, the other supported model (weight = 0.14) included distance to crops, with wild pigs selecting for areas closer to crops (Figure 3.3).

Discussion

Wild pigs have one of the most widespread distributions of any terrestrial mammal on the planet, with expanding populations throughout both their native and invasive ranges (Snow et al. 2016). As a result, damage by wild pigs is a global issue and the ability to determine factors influencing the timing and location of damage is crucial to mitigating their impacts, particularly in areas where wild pigs are invasive (Bleier et al. 2017). In this study we investigated habitat attributes associated with rooting damage by wild pigs across predominantly forested and agricultural landscapes in the southeastern U.S. Our results suggest that distance to roads, proximity to water, tree density, season, forest type, distance to crops, and presence of hard mast species are all important variables for predicting wild pig rooting. However, of these, tree density, season, and the presence of hard mast species were the most influential attributes contributing to the spatial distribution of wild pig rooting on the landscape. These findings are consistent with previous studies investigating the rooting damage, movement behavior, and diet of wild pigs (Ditchkoff et al. 2009; Robeson et al. 2018; Gray et al. 2020; Clontz et al. 2021), and suggest wild pig rooting is most concentrated in areas of high wild pig activity.

Wild pigs have been documented to preferentially select hard mast and green vegetation over subterranean tubers and invertebrates when available (Fournier-Chambrillon et al. 1995; Massei et al. 1996). While we did not implement a fall survey due to extensive leaf drop during the fall while mast would be on the ground, our winter survey encompassed damage from the previous fall (up to six months prior). Thus, the more extensive damage observed during winter likely reflects wild pig selection of hard mast, coupled with the reduced availability of green vegetation. Indeed, dietary studies of wild pigs have shown increased consumption of mast and sub-surface forage during the fall and winter as agricultural sources and green vegetation become scarce (Seward et al. 2004; Wilcox et al. 2009). In addition, the positive association between proximity to crops and rooting observed on the POA properties likely reflects a selection for forested areas near crops. This is supported by previous research on wild pigs and wild boar that observed increased crop damage in fields adjacent to forested habitats (Herrero et al. 2006; Wilber et al. 2019; Boyce et al. 2020).

Distance to roads, though not significant in any models, was associated with wild pig damage in both agricultural and forested ecosystems surveyed in our study, with wild pigs more likely to root in areas farther from roads. Roads can negatively affect wildlife by creating barriers to movement and causing mortality through vehicle collisions, however, the spread of invasive species like wild pigs can also be exacerbated by roads by providing corridors for movement (Forman et al. 2003; Coffin 2007; Ballari et al. 2013; Beasley et al. 2014; Clontz et al. 2021). In a highly mixed agricultural landscape, roads have been documented as being a deterrent and barrier for wild pigs, especially paved or highly trafficked roads (Wyckoff et al. 2012). For example, Boyce et al. (2020) found crop damage was negatively associated with areas near roads. In many areas roads are a direct source of mortality due to collisions with vehicles, (Morelle et al. 2013; Beasley et al. 2014), but also facilitate opportunistic hunting by landowners and managers.

The importance of water sources in influencing the distribution of wild pig rooting is unsurprising as pigs often concentrate movements near wetlands and riparian habitats due to the availability of foraging and wallowing habitats (Wood et al. 1980; Eckert et al. 2019; Clontz 2021). In addition to productive foraging areas, wild pigs use water features such as wetlands, streams, and ponds for wallowing, which is important for thermoregulation (Bracke 2011). Given the preference of wild pigs to concentrate activity around water sources and dense vegetation, wetlands are particularly vulnerable to damage by wild pigs. When water sources begin to dry out, wild pigs can become concentrated around remaining water sources such as wetlands, thus focusing damage within smaller areas. Wetlands are particularly vulnerable, as species and communities that are wetland specialists, many of which are threatened, endangered, or have restricted distributions, are likely to be particularly impacted by more localized damage by wild pigs (West et al 2009; Bengsen et al 2014). Specialized species which are immobile and have stages in their lifecycle that are inseparable from water sources may be at particular risk in these fragile ecosystems. In addition to direct impacts to riparian and wetland habitats through rooting and wallowing, wild pig use of water sources is concerning as pigs are known carriers of diseases that be transmitted to other wildlife, livestock, and humans (Brooks et al. 2020).

Both hardwoods (forest type) and tree density were important variables in characterizing the distribution wild pig rooting damage across our study areas, with more extensive rooting by wild pigs in areas with lower tree densities and areas dominated by hardwoods. Although wild pigs are ecological generalists, they exhibit spatio-temporal differences in resource selection that reflect underlying biological needs (Gray et al. 2020). Wild pig movements and rooting damage are often concentrated within forested areas, especially those dominated by hardwoods, which provide access to nutritional hard mast and dense cover (Singer et al. 1981; Hayes et al. 2009; Wilber et al. 2019; Gray et al. 2020). In the southeastern U.S., evergreen plantings generally have higher tree densities than hardwoods without the additional forage benefits, and higher canopy cover density that hardwoods supply for wild pigs. Hardwood habitats are also often associated with wetlands or water sources in many areas the southern U.S., which wild pigs preferentially select for (Clontz et al. 2021). Thus, evergreen areas with high tree density may be less desirable to wild pigs for rooting relative to less hardwood habitats that provide more forage opportunities.

Management Implications

Our results indicated that season as well as both broad and fine-scale habitat attributes and other landscape features such mast tree presence and tree density were all important factors influencing areas selected by wild pigs for rooting. While our general findings are consistent with previous literature on wild pig habitat selection and rooting damage, fine-scale patterns like tree density and mast tree presence provide further insight into the importance of environmental attributes critical to an invasive species like wild pigs that may be overlooked in coarse-scale resource selection approaches (Roever et al. 2014). Knowledge of attributes important in influencing where and when rooting will occur can serve as useful predictors when investigating areas for potential wild pig incursions as populations continue to expand. This information will also help in tailoring control efforts when resources are limited, or when calculating the potential effects of wild pigs across a landscape. Managers could use the results of this study to set up early detection and monitoring protocols in riparian areas and forested areas proximal to crop fields, particularly areas with hard mast to maximize efficiency. Our results also suggest wetland specialists may be particularly vulnerable to habitat damage or direct predation by wild pigs, and efforts to control wild pig populations should target these areas.

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Supporting Information

Table 3.1. Habitat attributes measured at wild pig (*Sus scrofa*) rooting damage locations, South Carolina, 2020-2021.

Variable (Abbreviation)	Description
Season (Se)	Season (Winter or Summer)
Veg (Ve)	Ground vegetation cover (%)
Stem (St)	Woodie stem density (number/m^2)
Understory (Un)	Dominant understory species
Tree (Tr)	Tree density (number/m^2)
Mast (Ma)	Mast presence or absence
Water (Wa)	Distance to water (m)
Forest (Fo)	Forest type (Hardwoods or Evergreen)
Roads (Ro)	Distance to roads (m)
Crops (Cr)	Distance to crops (m)

Table 3.2. Generalized linear mixed model results including the number of variables (K), Akaike's Information Criterion (AIC), ΔAIC, model weight, cumulative model weight, and log likelihood (LL) evaluating the influence of habitat attributes on wild pig (*Sus scrofa*) rooting damage on the Savannah River Site, South Carolina, USA.

*Model	K	AIC	Δ AIC	AIC Weight	Cumulative Weight	LL
Se, Fo, Wa, Ro, Tr, Ma	8	334.00	0.00	0.81	0.81	-158.73
Fo + Se	5	338.07	4.07	0.11	0.92	-163.92
Ro, Wa	4	341.24	7.25	0.02	0.94	-166.55
Wa + Se	4	342.50	8.50	0.01	0.95	-167.18
Se,Fo,Wa,Ro,Tr,Ma + Se	12	342.72	8.72	0.01	0.95	-158.76
Tr, Ma + Se	6	342.90	8.90	0.01	0.96	-165.29
Wa, Ro, Tr	5	343.19	9.19	0.01	0.97	-166.48
Null model	2	343.59	9.59	0.01	0.98	-169.77
Tr, Ro	4	343.72	9.72	0.01	0.98	-167.79
Ro, Wa + Se	6	343.95	9.95	0.01	0.99	-165.82
Tr, Ma, Wa, Ro + Se	10	344.08	10.08	0.01	0.99	-161.62
Tr, Fo, Ro + Se	8	344.32	10.32	0.00	1.00	-163.88
Tr, Ro + Se	6	347.52	13.52	0.00	1.00	-167.60
Wa, Ro, Tr + Se	8	347.78	13.78	0.00	1.00	-165.62
Master model	39	356.50	22.51	0.00	1.00	-132.53

Fo, Un	32	362.79	28.79	0.00	1.00	-144.98
Se, Ve, St, Un, Tr, Ma, Wa, Fo, Ro + Se	33	364.63	30.63	0.00	1.00	-144.60
Fo,Un+Se	48	386.64	52.64	0.00	1.00	-134.77
St, Ve ,Un + Se	50	394.71	60.71	0.00	1.00	-135.82
Master:season model	60	401.25	67.25	0.00	1.00	-123.28

*Season (Se), vegetation cover (Ve), woody stem density (St), dominant understory species (Un), tree density (Tr), mast tree presence (Ma), distance to water (Wa), forest type (Fo), distance to roads (Ro)

Table 3.3. Generalized linear mixed model results including number of variables (K), Akaike's Information Criterion(AIC), distance from the lowest AIC (Δ AIC), AIC model weights, cumulative model weights, and log likelihood (LL) used to predict wild pig rooting damage habitat selection on private properties in South Carolina, USA.

*Model	K	AIC	Δ AIC	AIC Weight	Cumulative Weight	LL
Tr, Ro	5	368.09	0.00	0.32	0.32	-178.94
Tr, Ro, Cr	6	369.78	1.69	0.14	0.46	-178.74
Tr, Ma, Cr	6	370.46	2.37	0.10	0.56	-179.08
Tr, Ma, Wa, Fo, Ro	8	371.09	3.00	0.07	0.63	-177.28
Wa, Ro, Tr	7	371.28	3.19	0.07	0.70	-178.44
Wa, Ro, Tr, Cr	7	371.28	3.19	0.07	0.77	-178.44
Tr, Fo, Ro, Cr	7	371.44	3.36	0.06	0.83	-178.52
Tr, Ma, Wa, Ro, Cr	8	371.86	3.77	0.05	0.87	-177.67
nullmodel	3	372.16	4.07	0.04	0.92	-183.04
Ro, Wa	5	373.07	4.99	0.03	0.94	-181.43
Tr, Ma, Wa, Fo, Ro, Cr	9	373.17	5.08	0.03	0.97	-177.26
Wa, Cr	5	374.66	6.57	0.01	0.98	-182.22
Ro, Wa, Cr	6	375.03	6.94	0.01	0.99	-181.36
Fo, Cr	5	375.41	7.32	0.01	1.00	-182.59
Fo, Un	67	449.72	81.63	0.00	1.00	-134.85
St, Ve, Un	68	452.54	84.45	0.00	1.00	-134.45

Fo, Un, Cr 68	68	453.29	85.20	0.00	1.00	-134.83
St, Ve, Un, Cr	69	456.15	88.06	0.00	1.00	-134.43
mastermodel	74	458.48	90.40	0.00	1.00	-126.18

*Vegetation cover (Ve), woody stem density (St), dominant understory species (Un), tree density (Tr), mast tree presence (Ma), distance to water (Wa), forest type (Fo), distance to roads (Ro), distance to crops (Cr)

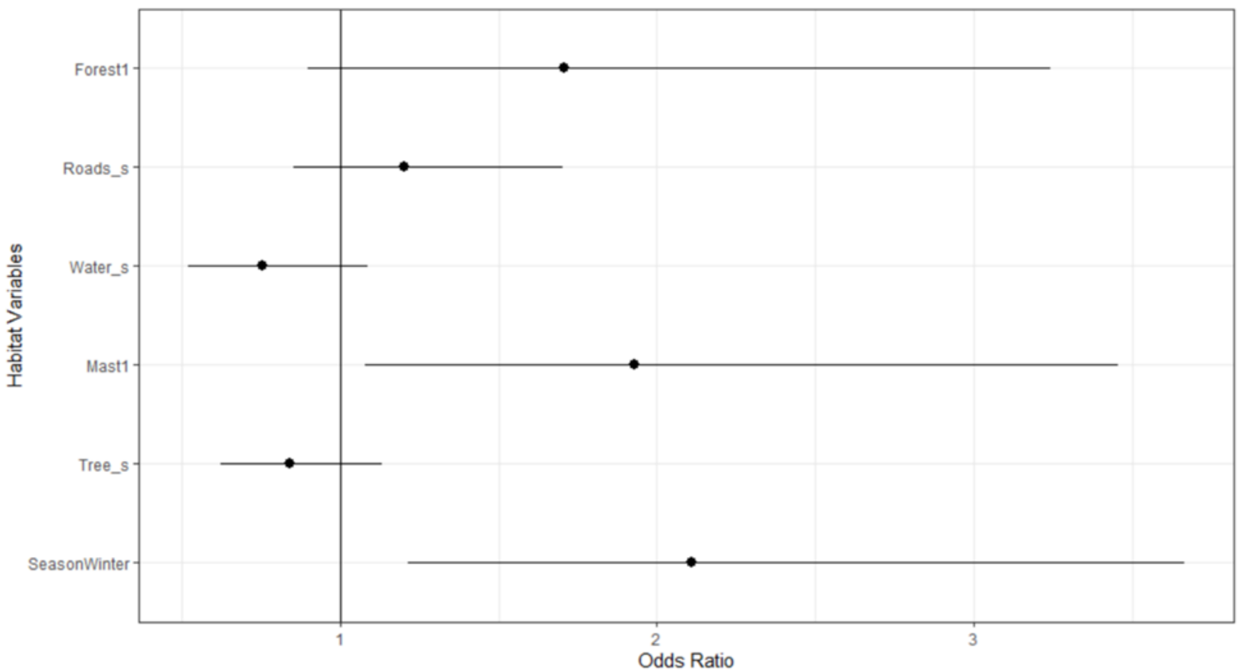

Figure 3.1. Predictive odds of the top Savannah River Site generalized linear mixed model with 95% confidence intervals. Habitat variables include forest type: hardwoods, distance to roads, distance to water, mast tree presence, tree density, and season: winter. Bars represent 95% confidence intervals. In cases where the confidence interval crosses 1, the variable is considered not significant.

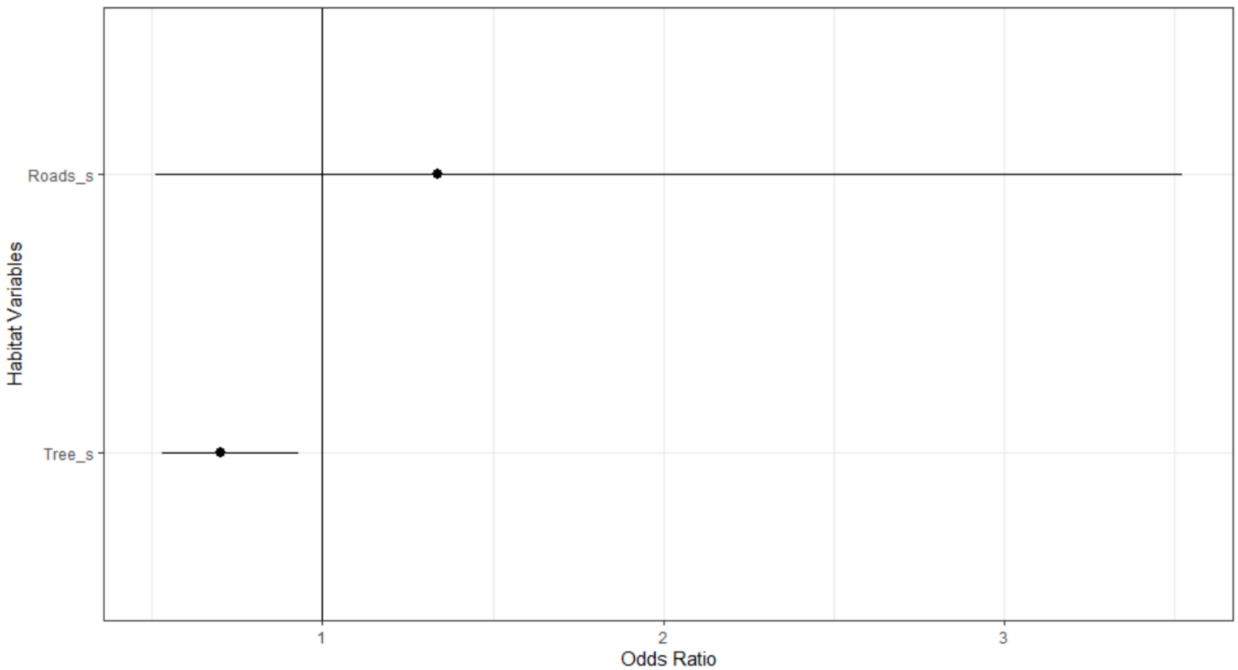

Figure 3.2. Predictive odds of the top privately owned agricultural property generalized linear mixed model with 95% confidence intervals. Habitat variables include distance to roads and tree density. Bars represent 95% confidence intervals. In cases where the confidence interval crosses 1, the variable is considered not significant.

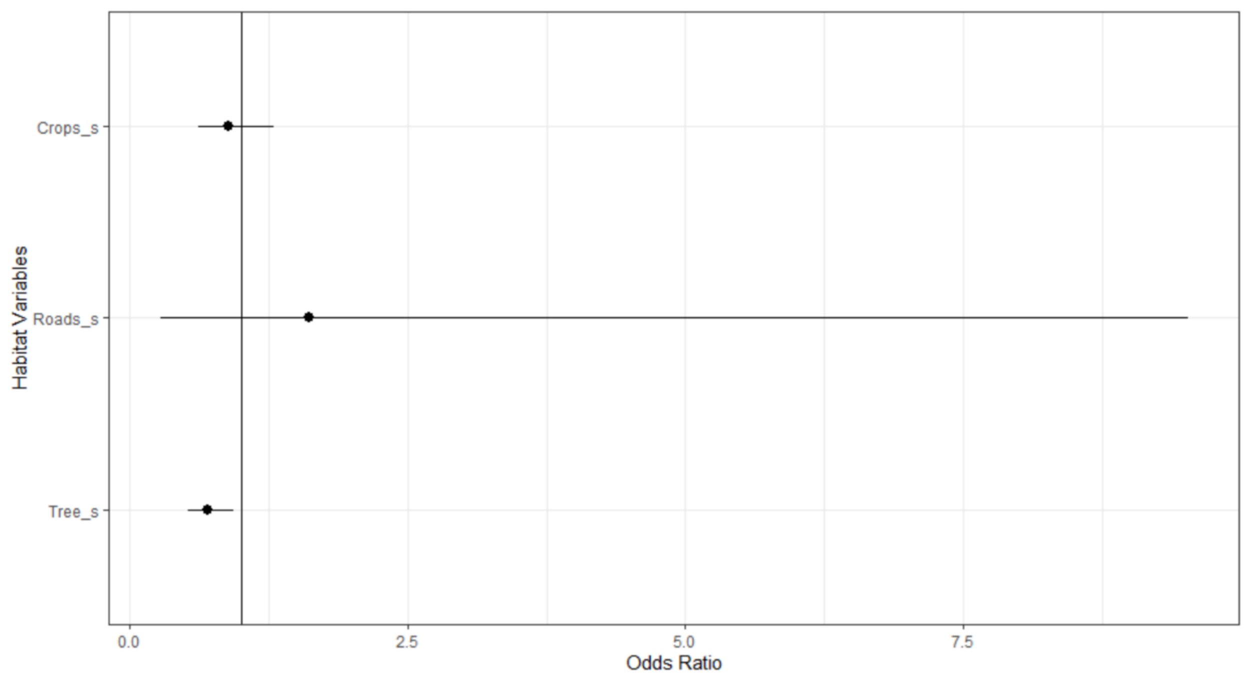

Figure 3.3. Predictive odds of the supported (<2 ΔAIC from top model) privately owned agricultural property generalized linear mixed model with 95% confidence intervals. Habitat variables include distance to roads, tree density, and distance to crops. Bars represent 95% confidence intervals. In cases where the confidence interval crosses 1, the variable is considered not significant.

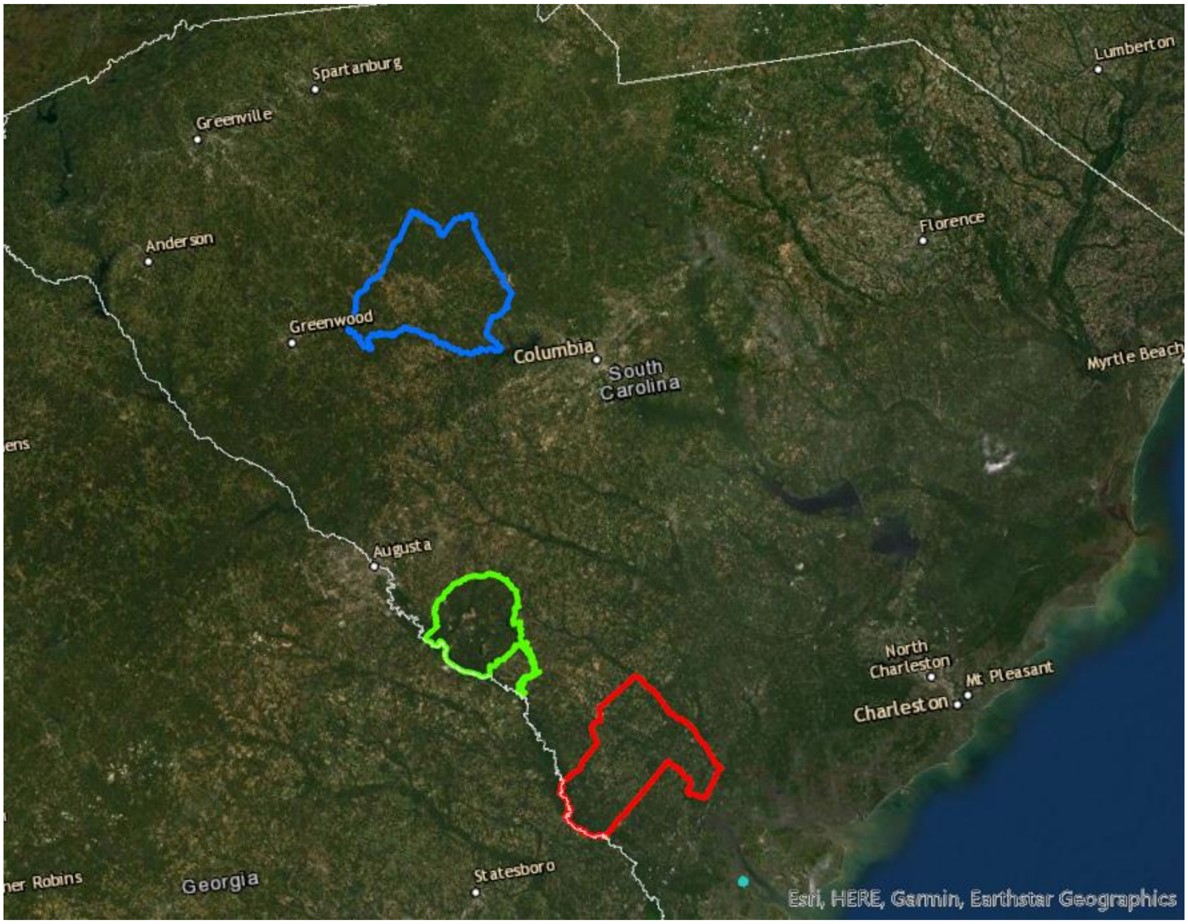

Figure 3.4. Map of South Carolina, USA, showing the (Green) Savannah River Site (SRS), (Red) Hampton County, and (Blue) Newberry County.

Figure 3.5. Examples of wild pig (*Sus scrofa*) rooting damage found on the Savannah River Site (SRS) and privately owned agricultural properties during 2020 while conducting transect surveys in South Carolina, USA.

CHAPTER 4

CONCLUSIONS

Despite the significant cost of wild pig (*Sus scrofa*) control and the extensive damage to both agriculture and the environment caused by this species, there are still significant gaps in our understanding of the impacts of control efforts on changes in population size and damage. In addition, spatial and temporal patterns with which damage occurs across a landscape are only just beginning to be understood. This lack of data largely stems from the urgency of wild pig control needs due to the sudden expansion of wild pig ranges across introduced areas, which often requires resources to be focused on management efforts over monitoring. In this thesis, I quantified changes in wild pig population size, agricultural damage, and environmental damage across numerous sites in South Carolina, USA. I also quantified patterns of wild pig environmental damage in relation to both large and fine scale habitat attributes across both predominantly forested and mixed-agricultural landscapes in South Carolina, USA. The methods used in this study can be applied to wild pig and wild boar populations across the globe, as well as beyond wild pigs to other invasive species that cause significant damage.

In Chapter 2, I monitored wild pig populations, crop damage, and environmental damage across 17 POA properties in conjunction with wild pig removal conducted on these sites. Populations were estimated using a relative abundance index and n-mixture models based on baited camera surveys across 17 properties prior to control and twice annually for up to 18 months. Environmental damage was quantified by conducting transect surveys across all properties both before and subsequent to control efforts. Agricultural damage was estimated from landowner survey response data, and only included damage attributed to wild pigs. I compared pre-control crop and environmental damage to those measured one year later after control methods were implemented. Removal efforts by the USDA-APHIS-WS over the two years (2020-2021) reduced the wild pig populations by 76% (Chapter 2) on average per property. This substantial population reduction corresponded to a similar significant reduction in agricultural damage and environmental rooting damage (78% and 94% respectively) one year after the removal efforts started. Control programs like the FSCP have proven that concentrated removal efforts are effective at decreasing wild pig populations. Not only do these programs serve to take highly invasive species like wild pigs off the landscape, but secondary effects such as the reduction in agricultural damage and the reduction in environmental damage increase the value of these programs.

In Chapter 3, I quantified wild pig damage on both the SRS and POA properties to identify seasonal changes and habitat attributes associated with rooting damage. Wild pig damage was quantified by conducting damage transect surveys and collecting information on habitat attributes associated with damaged and control sites. I tested a series of coarse and fine scale landscape attributes associated with damage sites to determine their effect on the presence of wild pig damage, and to discover if any attributes were important predictors of where damage occurred. On the predominantly forested SRS I found that hardwoods, distance to roads, distance to water, mast tree presence, and tree density were most associated with damage, and that wild pigs caused more extensive rooting damage in winter. Rooting also tended to occur more where mast trees were present. Wild pigs also selected for areas dominated by hardwoods, farther from roads, closer to water, and in less tree dense areas when rooting. On POA properties, I found that distance to roads, distance to crops, and tree density were most associated with damage. Wild pig damage was more concentrated in areas with lower density of trees as well as areas closer to crops and farther from roads on POA properties.

Collectively, the results of this thesis will increase the efficiency of wild pig management efforts from local landowners to the national level. Determining the efficacy of control efforts is critical to demonstrate whether resources and effort allocated to removal efforts are resulting in sufficient reductions in wild pig populations. My data suggests that investments made to control wild pig populations on private lands can be successful in not only reducing populations below threshold targets necessary to effectively manage populations given their high reproductive capacity, but also reducing the economic and ecological damages caused by wild pigs. More research is needed into the extent to which control programs must be maintained to achieve desired outcomes, as well as the effects of control programs on surrounding areas. Similarly, research on the impact of safe-havens where management activities may be prohibited or discouraged are needed to establish realistic and sustainable management goals. Prior studies have demonstrated that wild pigs preferentially use wetland or other riparian sites. However, my results suggest wild pigs also may concentrate rooting in these areas, suggesting direct (i.e. predation) and indirect (i.e. habitat destruction/modification) impacts of wild pigs may be most pronounced in these areas. The results of my rooting surveys may also help target specific areas of high interest or specific locations on a property that have a higher risk of wild pig damage. This in turn can result in higher efficiency of monitoring and removal efforts by landowners and managers.